Mackenzie et al.

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Mid-Atlantic)

AMERICAN SHAD

Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Mid-Atlantic)

AMERICAN SHAD

by

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(°F - 32)	Celsius degrees

CONTENTS

ACKNOWLEDGMENTS

The authors thank Christine M. Moffitt, Idaho Cooperative Fishery Research Unit, University of Idaho; Richard J. Neves, Virginia Cooperative Fishery Research Unit, Virginia Polytechnic Institute and State University; and Roy W. Miller, Division of Fish and Wildlife, Dover, Delaware, for reviewing portions of the manuscript.

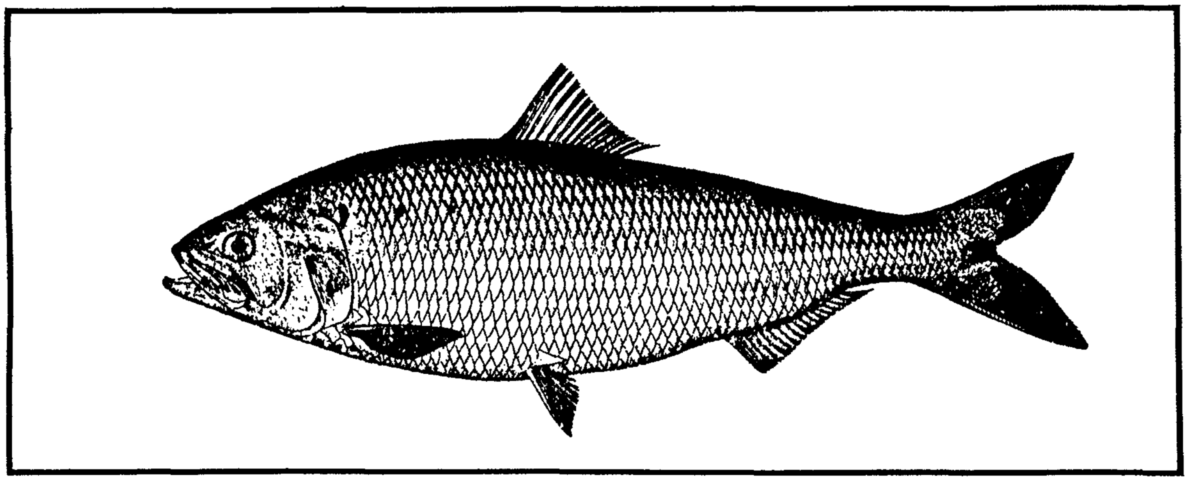

Figure 1. The American shad.

AMERICAN SHAD

NOMENCLATURE/TAXONOMY/RANGE

Scientific name . . Alosa sapidissima (Wilson)
Preferred common name . . . American shad (Figure 1).
Other common names . . shad, alose, common shad, Atlantic shad, North River shad, Potomac shad, Connecticut River shad, Delaware shad, Susquehanna shad, white shad, buck shad (males only), poplarback shad (Scott and Crossman 1973).
Class . . . . Osteichthyes
Order . . . . Clupeiformes
Family. . . . . Clupeidae

Geographic range: American shad are anadromous. They are distributed along the Atlantic coast from Newfoundland to Florida, and are most abundant from Connecticut to North Carolina. In the mid-Atlantic region the American shad ascend essentially all major rivers, but abundance in some rivers is limited by pollution or restricted by dams (Figure 2).

On the Pacific coast, the American shad was introduced into the Sacramento and Columbia Rivers in 1871, and the species is now established from southern California northward to Cook Inlet, Alaska, and the Kamchatka Peninsula in Asia.

MORPHOLOGY/IDENTIFICATION AIDS

Body elongate, strongly compressed laterally, and rather deep, its depth 17%-19% of total length (TL) (Leim 1924; Bigelow and Schroeder 1953; Scott and Crossman 1973). Head broadly triangular, 22%-24% of TL. Gill membranes free from isthmus. Eye moderate, adipose eyelid well developed, diameter of eye 27%-32% of head length (HL); snout moderate, length 27%-32% HL; interorbital width 19%-22% of HL. The anterior end of the lower jaw not especially thick or heavy and somewhat pointed, and fitting easily into a deep notch in upper jaw so that the jaws are about equal when the mouth is closed. The upper outline of the lower jaw slightly concave. Maxillary extending to posterior margin of eye. Teeth small, weak, and few in

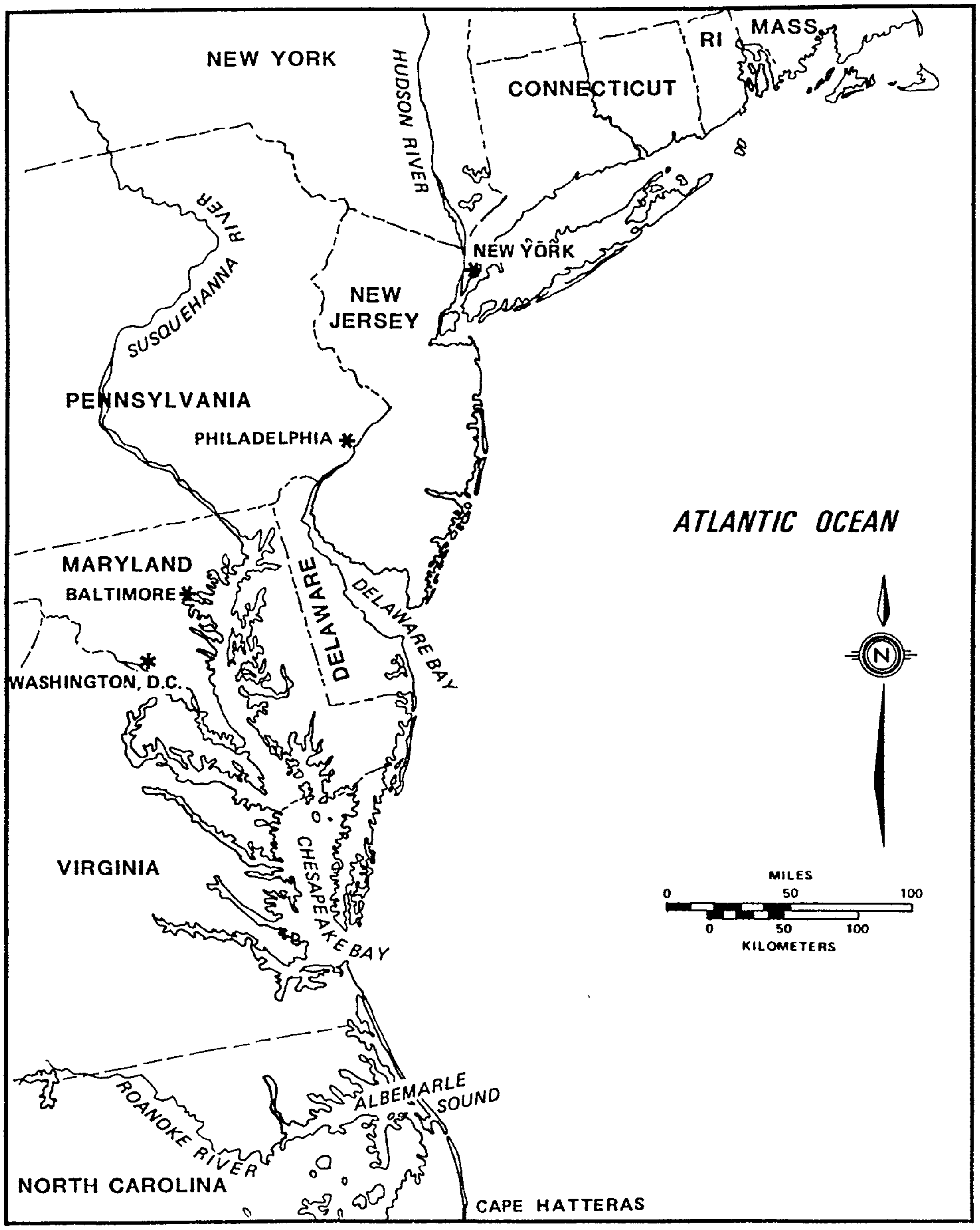

Figure 2. American shad are distributed along the coast of the Mid-Atlantic Region from Massachusetts to North Carolina, but are most abundant in this region along the coast from Connecticut to North Carolina. They ascend essentially all major rivers but may be limited in some rivers by pollution or restricted by dams.

number on premaxillary and mandible (lost completely in the adult) and absent on the roof of the mouth. Gill rakers on lower limb 59-73; branchiostegal rays 7,7 (rarely 7,6). Fins soft rayed: dorsal-1, height moderate, base short, 11%-13% of TL, rays 15-19, usually 17-18; caudal, distinctly forked; anal-1, base length greater than dorsal base, 13%-14% of TL, height shorter than dorsal height, rays 18-24, usually 20-22; pelvics, abdominal, small, length 9%-10% of TL, rays 9; pectorals, low on sides, length 14%-15% of TL, rays 14-18, usually 16. Scales, large, crenulate on posterior margin, deciduous. Lateral line poorly developed with about 50-55 scales. Ventral scutes well developed forming a sharp sawbelly, prepelvic scutes 19-23, usually 20-22, postpelvic scutes 12-19, usually 15-17. Vertebrae 53-59, usually 55-58. Peritoneal lining pale; pyloric caeca numerous and usually clustered on right side. Usually 4 to 6 black spots in horizontal row behind operculum. Size: average total length 380 mm; males up to 2.7 kg; females up to 3.6 kg, rarely to 5.4 kg.

REASON FOR INCLUSION IN THE SERIES

Historically, commercial fishing for American shad on the Atlantic coast has been intensive and widespread. Now the fishery has virtually collapsed and is important only in a few rivers (Connecticut R., Connecticut; Hudson R., New York; Neuse R., North Carolina; York R., Virginia) in the mid-Atlantic region. In the rivers that support strong runs, sport fishing for shad is more important than commercial fishing. Federal and State agencies have initiated management programs aimed at restoring American shad to their former range and abundance. The American shad is a natural resource that should be considered for protection in coastal and riverine development projects.

LIFE HISTORY

Spawning

The American shad is an anadromous fish that lives several years in the ocean and then returns to its river of origin to spawn. At one time, the species probably spawned in virtually every accessible river and tributary along the Atlantic coast of North America.

The freshwater spawning migration in winter, spring, or summer is timed to correspond to favorable river water temperatures. Shad usually migrate far enough upstream so that the eggs drift downstream and hatch before reaching saltwater. In one study in the Connecticut River, low river temperatures may have delayed the maturation of gonads causing the shad to migrate farther upstream to spawn (Marcy 1976). Glebe and Leggett (1981) reported that the gonads of American shad mature prior to entering the Connecticut River.

American shad spawn as early as mid-November in Florida and as late as July in some Canadian rivers. Males arrive at the spawning grounds before females (Chittenden 1975). Water temperature is the primary factor that triggers spawning, but photoperiod, flow velocity, and water turbidity also exert some influence (Leggett and Whitney 1972).

Although shad eggs in Virginia streams become abundant after the water temperature reach 12°C (Massman 1952), most spawning is from 13° to 20°C (Walburg and Nichols 1967). In North Carolina, peak spawning is at water temperatures near 20°C (Sholar 1976).

The diameter and abundance of shad eggs collected in plankton nets in the Pamunkey River, Virginia, indicate that spawning takes place at all hours of the night and day but is more intense from noon to midnight (Massman 1952). According to Miller et al. (1971, 1975), spawning begins in the evening between 1900 h and 2000 h and peaks between 2100 h and 2300 h in the Delaware River. After 0100 h, most of the spawning subsides. On overcast days, spawning begins earlier than on clear days, which supports the hypothesis that the daily onset of spawning is regulated by light intensity (Miller et al. 1982).

Group spawning involving several males and a female has been observed (Marcy 1972). The spawning fish swim vigorously at the surface, forming a closely packed circle. Eggs are released into the water and then fertilized by the males (Marcy 1972; Scott and Crossman 1973).

Shad spawn in main streams of North Carolina rivers over sand shoals where there is sufficient current to keep the eggs suspended in the water column (Sholar 1976). Shad spawn over sand, silt, muck, gravel, and boulder substrates (Mansueti and Kolb 1953; Walburg 1960; Leggett 1976). They spawn in water depths about 1 to 10 m (3 to 30 ft) but most often less than 3 m (10 ft) (Walburg and Nichols 1967). The current in spawning areas ranges from about 0.5 to 3 ft/s (Walburg and Nichols 1967; Marcy 1972).

The percentage of shad that spawn more than once increases from south to north (Table 1). For example, shad in rivers south of Cape Fear, North Carolina, die after spawning, but in more northerly rivers some shad survive spawning to spawn again. Shad may return to spawn for up to 6 years (Table 2). The percentage of repeat spawners ranges from 0% for the St. Johns River, Florida, south of Cape Fear, North Carolina, to 73% in the St. John River, New Brunswick (Carscadden and Leggett 1975a, 1975b). The Delaware River, unlike other mid-Atlantic coast shad rivers, has few repeat spawners (1.5% to 6.5%) according to Chittenden (1975). He suggests that the probable causes for the scarcity of repeat spawners there are pollution and overfishing.

Table 1. The percent of repeat spawners in American shad spawning runs in Atlantic coast rivers (Leggett and Carscadden 1978).

River and location	Latitude of river (°N)	Repeat spawners(%)
Miramichi (NB)	49	64
St. John (NB)	45	73
Connecticut (CT)	41	63
Hudson (NY)	41	57
Delaware[a] (DL)	40	6
Susquehanna (VA)	40	37
Potomac (VA)	38	20
York (VA)	37	24
James (VA)	37	27
Neuse (NC)	35	3
Edisto (SC)	33	0
Ogeechee (GA)	32	0
St. Johns (FL)	30	0

[a] Chittenden (1975).

Fecundity and Eggs

The American shad has a relatively high fecundity (116,000 to 659,000 eggs per female; Table 2). Many eggs fail to fertilize and only a small percentage of the fertilized eggs hatch. High egg mortality has been attributed to failure to fertilize, suffocation, fungus infection, and predation (Leach 1925; Mansueti and Kolb 1953).

The fecundity of spawners decreases from south to north (Table 3). These trends in fecundity are independent of age and size.

Unfertilized eggs are irregularly round in form and are about 1.8 mm in diameter; fertilized, waterhardened eggs are 2.5 to 3.5 mm in diameter and

Table 2. Lengths, weights, ages, and range of the number of eggs of American shad in the spawning populations of seven Atlantic coast rivers of the United States, 1951-1959 (Walburg and Nichols 1967).

River	Fork length (mm)	Body weight (kg)	Age (years)	Range of number of eggs per female (x 1,000)
Hudson (NY)	355-556	0.8-3.0	3-9	116-468
Potomac (VA)	460-505	1.4-2.4	5-6	267-525
York (VA)	399-470	1.1-2.1	4-6	169-436
Neuse (NC)	447-498	1.8-2.7	4-6	423-547
Edisto (SC)	465-498	1.6-2.2	4-5	360-480
Ogeechee (GA)	457-475	1.7-2.2	4-6	359-501
St. Johns (FL)	368-460	0.6-1.8	4-6	277-659

Table 3. Mean virgin (first time spawners) and lifetime fecundities of American shad populations from five Atlantic coast rivers, 1958-1973 (Leggett and Carscadden 1978).

River	Virgin fecundity	Lifetime fecundity
St. Johns (FL)	406,000	406,000
York (VA)	259,000	327,000
Connecticut (CT)	256,000	384,000
St. John (NB)	135,000	273,000
Miramichi (NB)	129,000	258,000

are transparent, pale pink, or amber (Marcy 1976; Miller et al. 1982). Fertilized eggs are slightly heavier than water and are nonadhesive. The rate of development of shad eggs is linearly related to temperature (Mansueti and Kolb 1953). Eggs hatch in 8 to 12 days at 11° to 15°C; 6 to 8 days at 17°C; and 3 days at 24°C (Bigelow and Schroeder 1953; Scott and Crossman 1973). No viable eggs develop at water temperatures above 29°C (Bradford et al. 1966).

Larvae to Adults

American shad yolk-sac larvae are about 6 to 10 mm long (TL) at hatching and 9-12 mm TL when the egg yolk is absorbed (Marcy 1976). Initially the larvae 9-27 mm TL are planktonic (Mansueti and Hardy 1967; Jones et al. 1978). They reach the juvenile stage when about 25 to 28 mm long and about 4 weeks old (Jones et al. 1978). Juveniles spend the first summer in the river feeding on crustaceans and aquatic insects at the surface or in the water column (Leim 1924; Walburg 1957; Levesque and Reed 1972).

In the fall, juveniles (75 to 125 mm long) migrate down the rivers to brackish water and then to the sea. A decrease in river water temperature seems to trigger the migration (Chittenden 1972). Juvenile shad migrate seaward first in northern rivers and progressively later in southern rivers (Leggett 1977). Juvenile shad leave the St. Johns River, Florida, as the water cools to 15.5°C (Walburg 1960). In the Delaware River, shad begin moving downstream when the water temperature drops to about 20°C; the movement peaks at 15°C (Sykes and Lehman 1957). In the Connecticut River, downstream migration peaks late in September and October. Peaks for the Upper Delaware River and the Chesapeake Bay are late October and late November, respectively. Once in the ocean, the shad remain there until they mature.

Males become sexually mature when they are 3 to 5 years old and the females mature at 4 to 6 years old (Leim 1924). Most of the male first-time (virgin) spawners in the Neuse (North Carolina) and Susquehanna (Maryland) Rivers are 4 years old (LaPointe 1958). The majority of female virgin spawners are 4 to 5 years old. Shad are known to complete their entire life cycle in only one freshwater system: Millerton Lake, a reservoir on the San Joaquin River, California (Lambert et al. 1980).

Morphological characteristics for distinguishing shad larvae from other larvae of similar species are described by Jones et al. (1978).

Ocean Migration

The American shad in the mid-Atlantic region form large schools and undertake extensive ocean migration (Leggett and Whitney 1972). Shad from all Atlantic coast rivers spend the summer and fall in the Gulf of Maine (Talbot and Sykes 1958). This congregation includes immature shad and spawned-out adults from rivers north of Chesapeake Bay. Shad are apparently scattered along the mid-Atlantic coast during the winter (Talbot and Sykes 1958; Walburg and Nichols 1967). Migrating American shad seek bottom water temperatures between 3° and 15°C but probably prefer temperatures between 7° and 13°C (Neves and Depres 1979).

In early spring, the schools of shad migrate toward the coast. Those returning to rivers south of Cape Hatteras follow the Gulf Stream to remain within the 3° to 15°C bottom isotherm. Those migrating to rivers north of Cape Hatteras later in the spring follow a route farther seaward into the Middle Atlantic Bight where water temperatures have risen sufficiently. Tag returns indicate that some schools migrate north along the coast (Neves and Depres 1979).

American shad migrate as much as 21 km/day in Chesapeake Bay and the Bay of Fundy (Leggett 1977). Some migrate up to 3,000 km during the spring or fall migration.

A large majority of American shad return to their natal river to spawn. Homing behavior involves both olfaction and rheotaxis (Dodson and Leggett 1974). The homing mechanism is sufficiently robust to perpetuate migrations even after major changes in water flow, such as below a hydroelectric dam.

GROWTH CHARACTERISTICS

American shad live to be 5 to 7 years old and most weigh between 1 to 3 kg. The oldest shad reported for the United States was 11 years of age and 584 mm long (Scott and Crossman 1973). Factors that affect growth sometimes can be identified by examining fish scales. Slow growth in the winter causes growth rings on scales to be close together; these winter marks (annuli) can be used to age fish. Judy (1961) verified the scale method for aging American shad. He also noted a mark on the scales that formed when the juveniles left fresh water, and described marks that formed at spawning. Shad grow about 100 mm/yr until sexually mature; after maturity, growth slows (Table 4).

Table 4. The average total lengths of shad and annual growth increments (mm) for ages I to VII in the Bay of Fundy (Leim 1924).

Growing Season	Age	Length	Increment
1st	I	120	-
2nd	II	240	120
3rd	III	320	80
4th	IV	400	80
5th	V	470	70
6th	VI	520	50
7th	VII	570	50

THE FISHERY

History

In the 19th century, extensive fisheries for shad developed along the entire Atlantic coast from the St. Johns River, Florida, to the St. Lawrence River, Canada. Major types of gear were drift and staked gill nets, pound nets, haul seines, weirs, fyke nets, bow nets, and dip nets. The estimated U.S. Atlantic coast catch in 1896 was 22,680 metric tons (50 million lb). Between 1930 and 1960, the average annual catch was about 4,530 metric tons or 10 million lb (Figure 3). In 1983, landings were about 1,585 metric tons (3.5 million lb).

Commercial shad landings in Chesapeake Bay were traditionally the largest along the Atlantic coast (Table 5), but because of the closure of Maryland's shad fishery in 1980, the mid-Atlantic and South Atlantic catches have been greater. Dams, pollution, and overfishing have contributed to the decline of shad stocks.

Current Statistics

Rhode Island. American shad are an incidental part of the commercial catch in Rhode Island. Approximately 77,000 lb were landed in 1982 (Table 6). The Runnings and Warren Rivers support a small sport fishery. Shad

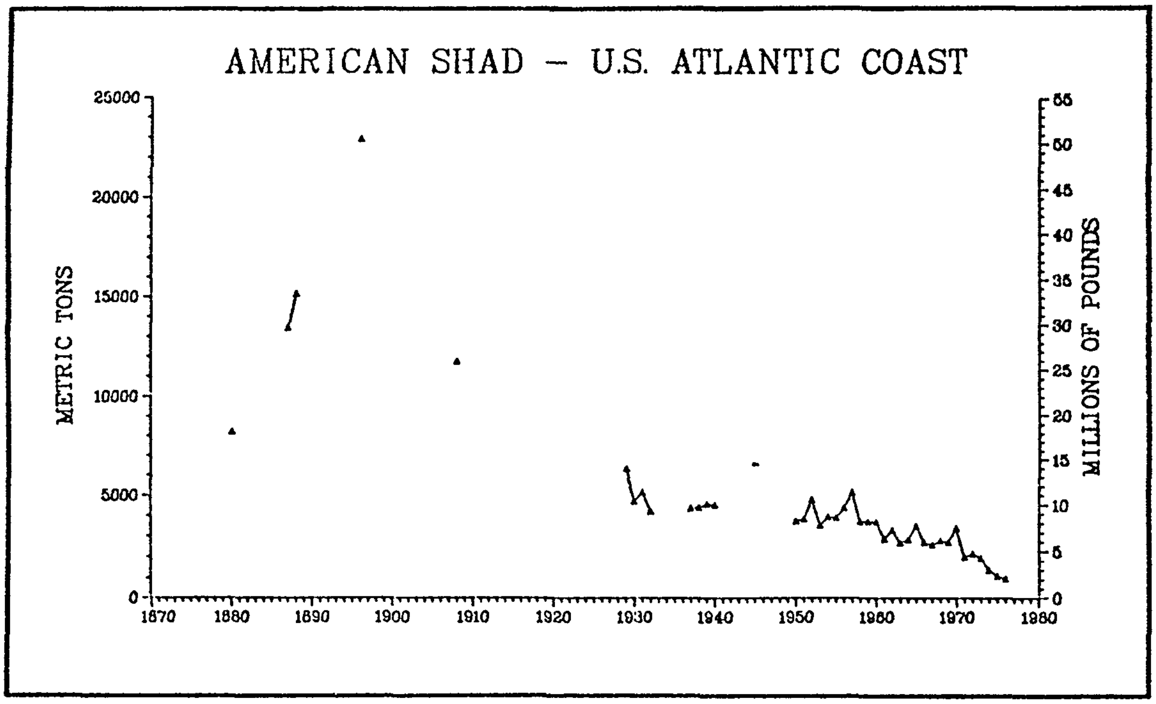

Figure 3. Landings of American shad, U.S. Atlantic coast, 1880-1976 (Walburg and Nichols 1967; updated and reproduced with permission from Public Service Electric and Gas Company, 80 Park Plaza, Newark, New Jersey 07101).

Table 5. The landings of American shad (x 1,000 lb) for different regions along the U.S. coast, 1960-83. Code: NE=New England, MA=Mid-Atlantic, CB=Chesapeake Bay, SA=South Atlantic, PC=Pacific Coast (1960-77, National Marine Fisheries Service, Statistical Digest; 1978-83, National Marine Fisheries Service, unpublished data).

	Coastal regions				
Year	NE	MA	CB	SA	PC
1960	432	1,237	2,682	1,614	456
1961	547	1,026	3,144	1,612	927
1962	470	841	3,795	2,167	1,586
1963	325	744	3,139	1,734	1,503
1964	320	721	3,541	1,687	818
1965	380	635	4,298	2,379	870
1966	279	379	3,564	1,736	1,347
1967	754	387	3,005	1,562	1,333
1968	218	379	3,508	2,052	862
1969	201	342	3,540	1,904	610
1970	186	314	5,151	1,851	724
1971	283	222	2,473	1,452	499
1972	264	375	3,014	1,091	709
1973	261	308	3,033	685	483
1974	257	294	1,789	655	511
1975	208	337	1,321	518	522
1976	412	322	1,006	320	481
1977	418	394	1,547	418	560
1978	361	245	1,322	976	545
1979	330	216	1,041	363	797
1980	253	406	998	839	277
1981	66	510	500	1,235	120
1982	403	757	590	1,033	429
1983	504	365	242	1,974	413

have been reintroduced unsuccessfully in the Pawcatuck River, in an attempt to restore a spawning population there; the river is currently closed to shad fishing.

Connecticut. The Connecticut River supports a modest commercial shad fishery. Most fishing is with drift gill nets below Hartford at night. Some fishing is done during the day when the water is turbid. Fyke, trap, and pound nets are not allowed in the river during the shad run. The primary market is for roe (eggs); males (buck shad) have little or no value. The State of Connecticut carefully regulates commercial fishing for shad on the Connecticut River. The season is open to commercial fishing from April 1 to June 15. During the season, fishing is prohibited from Friday sunset to Sunday sunset. Monofilament gill nets are prohibited and the gill nets used must have a minimum stretch measure of 5 inches. There are no size or sex restrictions. License holders must report their catch at the end of each fishing season.

Sportfishing for shad in Connecticut is permitted from April 1 to a closing date determined each year.

Table 6. Annual (1960-83) commercial landings (x 1,000 lb) of American shad from Rhode Island, Connecticut, New York, New Jersey, Maryland, and North Carolina (1960-77, National Marine Fisheries Service, Statistical Digest; 1978-83, National Marine Fisheries Service, unpublished preliminary data).

Year	Rhode Island	Connecticut	New York	New Jersey	Maryland	North Carolina
1960	3	421	472	694	1,336	702
1961	4	463	303	633	1,815	673
1962	7	456	243	480	1,575	765
1963	2	301	202	442	827	693
1964	3	278	141	430	890	640
1965	4	352	133	392	1,343	1,069
1966	23	242	81	242	1,133	701
1967	5	240	113	248	867	777
1968	2	212	126	241	958	842
1969	6	190	136	188	1,292	719
1970	12	173	106	195	1,039	953
1971	42	241	73	141	953	680
1972	14	249	103	263	957	468
1973	2	258	157	143	597	321
1974	7	247	164	122	220	369
1975	6	165	196	122	184	241
1976	3	392	186	100	110	167
1977	1	392	1	194	77	120
1978	1	332	2	160	87	402
1979	1	306	8	148	47	278
1980	2	207	114	292	24	199
1981	1	325	58	259	1	352
1982	77	283	73	334	9	412
1983	23	424	33	112	27	380

Angling and scoop nets are permitted in streams. The daily bag limit is six fish.

New York. The Hudson River has the only commercial American shad fishery of note in New York. Gill nets are the principal type of commercial gear used. Staked gill nets contribute about 70% of the gill net catch and drift gill nets contribute 30%.

New Jersey. Most commercial fishing (almost entirely with gill nets) in New Jersey is concentrated in Delaware Bay; there is no sport fishery in the bay. The only sport fishery begins about 90 mi up the Delaware River near Trenton, New Jersey. Shad from the Delaware River have been stocked into the Raritan River basin in an attempt to restore the once abundant runs there; however, all attempts of restoration have failed (Didun 1983).

Pennsylvania. There is no commercial fishery for American shad in Pennsylvania, but major restoration attempts are underway on the Susquehanna and Schuylkill Rivers where sport fishing for shad is currently banned. The estimated annual value of the sport fishery on the Schuylkill River fishery will be $1,200,000 if the goal of restoration is achieved (Mulfinger and Kaufmann 1980). Estimates of the annual value of the current sport fishery on the upper Delaware River range from $828,000 to $3,000,000 (Miller et al. 1982).

Delaware. The legal commercial gear in Delaware is 5- to 6-inch (stretch measure) gill nets. Fishing is allowed from March until early May. In the past 30 years, the fishery has shifted from the lower Delaware River, where drift gill nets were used, to Delaware Bay, where anchored gill nets predominate (Miller 1982). The increase in the commercial catch of American shad in the Delaware Estuary in recent years gives some evidence that the species is becoming more abundant (Table 7). The increase is attributed partly to recently completed pollution abatement projects in the lower Delaware River (Miller 1982). There is no sport fishery except for Nanticoke River and Broad Creek, tributaries to Chesapeake Bay. The fishing season for the Delaware waters of the Delaware Estuary is from June 10 to February 1.

Maryland. A sharp decline in the commercial catch of American shad in Maryland began in 1973 (Table 6). This led to the closing of all waters in Maryland to shad fishing with the exception of the Potomac River (which is regulated by the Potomac River Fisheries Commission) and coastal waters (Carter and Weinrich 1982).

Table 7. American shad catch (x 1,000 lb) and value (x 1,000 dollars) for Delaware and Virginia (Miller 1982; Jack Travelstead, Virginia Marine Resources Commission; pers. comm.).

Date	Delaware		Virginia	
	Catch	Value	Catch	Value
1960	38	6	1,349	234
1965	110	16	2,955	307
1970	13	1	4,112	315
1975	19	4	1,137	309
1976	36	8	896	284
1977	75	15	1,469	498
1978	70	20	1,235	212
1979	95	15	994	235
1980	96	31	974	353
1981	191	87	499	141
1982	333		585	180

Virginia. The biggest American shad fishery is along the Atlantic coast of Virginia. In 1982, 585,000 pounds were landed with a value of $180,028 (Table 7). Gill nets are the primary gear used.

North Carolina. In North Carolina, shad are caught by commercial and sport fishermen from late January to the end of March. The commercial fishery employs drift and staked gill nets, pound nets, and seines. The primary types of gear used on the Neuse River, which has the largest commercial catch, are staked and drift gill nets (Hawkins 1980).

Population Dynamics

Recruitment into the shad fishery is largely dependent on the size of the spawning stock and environmental factors that govern spawning success and survival. About 85% of the variation in the numbers of American shad that spawn in the Hudson River in any one year is largely dependent on the number of spawners 5, 4, and 1 year earlier (Talbot 1954). About 64% of the annual variation in the abundance of juvenile shad in the Connecticut River from 1966 to 1973 was directly related to the number of spawners; 22% was attributed to environmental factors, principally water temperature and river flow during the run (Marcy 1976).

The rate of exploitation is a major factor influencing changes in the abundance of shad in the Connecticut River (Leggett 1976). Because of the high value of shad eggs (roe), females in the spawning run are the main targets of the fishery.

The number of adults that survive the fishery in any one year is directly correlated with the numbers of fish produced in the next generation. This relationship is described by a stock-recruitment equation:

$$R = N_e^{0.7\ (1 - N/87)}$$

where R is recruitment and N is the parent stock in terms of egg numbers (Leggett 1976). Average annual mortality rates, calculated from tag-recaptures data, were about 70% for males and 71% for females from 1965 to 1973 in the Connecticut River (Leggett 1976).

The age structure of American shad returning to spawn in Delaware and North Carolina consists primarily of 4- and 5-year-old males and 5- and 6-year-old females (Table 8).

ECOLOGICAL ROLE

Foods

Apparently, young American shad in rivers feed mostly in the water column (Levesque and Reed 1972; Domermuth and Reed 1980). Early shad larvae feed mostly on cyclopoid copepods and tendipedids (Levesque and Reed 1972). The stomach contents of juvenile (35-85 mm FL x = 55 mm) shad in six Atlantic coast rivers (St. Johns, Florida; Ogechee, Georgia; Neuse, North Carolina; Pamunkey, Virginia; Hudson, New York; Connecticut, Connecticut) suggested that shad ate suitable organisms that were most available (Walburg 1957). In contrast, a study performed on the Connecticut River, Connecticut, by Domermuth and Reed (1980) demonstrated that juvenile shad (Tl = 28 to 132 mm x = 63.3 mm) were selective; i.e., most selected daphnia (51%) and bosmids (20%), whereas despite high abundance, copepods (8%) and benthos (0.1%) were consumed in small quantities.

After going to sea, juveniles and adults feed on a variety of small crustaceans, many of which are benthic organisms. Copepods and mysids constituted 90% of the diet of adult shad in the Bay of Fundy (Leim 1924). Adults also feed on small fishes, euphausids, fish eggs, and amphipods (Bigelow and Schroeder 1953; Scott and Crossman 1973). Most shad have a diel vertical migration that follows the diel migration of their principal food, zooplankton (Neves and Depres 1979). In a study off the coast of North Carolina, anchovies (<u>Anchoa hepsetus</u>) were in 12 of the 15 juvenile shad examined (87-141 mm), and 39 of 41 adults (Holland and Yelverton 1973). The stomachs also contained zooplankton under 5 mm (Holland and Yelverton 1973). This size was reported by Atkinson (1951) as being too small for shad gill rakers to retain.

Food was scarce in the stomachs of shad migrating upstream to spawn (Leim 1924). But in one experiment, migrating prespawning shad placed in a freshwater pond fed on artificial feed (Atkinson 1951).

Adult shad fed on mayflies in freshwater and their stomachs contained the remains of small fish (Chittenden 1976). Shad strike

Table 8. Age composition (%) of the spawning population of American shad in the Delaware River, Delaware (Chittenden 1975), and the Neuse River, North Carolina (Hawkins 1980).

Delaware			North Carolina		
Age	Number	%	Age	Number	%
	Males			Males	
II	1	0.0	III	16	5
III	8	2.6	IV	126	39
IV	236	76.1	V	151	46
V	62	20.0	VI	310	9
VI	3	0.0	VII	3	1
	Females			Females	
IV	50	13.7	IV	47	6
V	225	61.6	V	447	58
VI	88	24.1	VII	10	1
VII	2	0.0	VIII	1	0

artificial lures when in freshwater, a behavior unexplained.

Predators

Juvenile shad may be preyed upon by a variety of predators in freshwaters (Scott and Crossman 1973), but Leim (1924) was unable to demonstrate predation by either American eels (Anguilla rostrata) or striped bass (Morone saxatilis) in the Shubenacadie River, Nova Scotia. Seals prey on American shad, but adults probably have few enemies, except for humans (Scott and Crossman 1973).

Diseases

The American shad has the usual complement of parasites and diseases. Acanthocephala, parasitic copepods, distomes, nematodes, and trematodes have all been reported in or on shad (Scott and Crossman 1973). In the Connecticut River, the sea lamprey (Petromyzon marinus) and freshwater lampreys (Ichthyomyzon spp.) sometimes attach to adult shad (Walburg and Nichols 1967).

ENVIRONMENTAL REQUIREMENTS

Salinity

The American shad adapts readily to either freshwater or seawater during its anadromous migrations. The adults may spend two to three days in the estuary before entering the river (Leggett 1976). One test was made in this connection. Transfer of adult shad from seawater to freshwater over a 2.5 hour period caused physiologic stress and a mortality of 54% (Leggett and O'Boyle 1976).

Eggs are always deposited in freshwater and are believed to be intolerant of full-strength seawater. Leim (1924) suggests that shad eggs and larvae tolerate brackish water with a salinity as high as 15 ppt.

Temperature

Spawning runs into rivers (Columbia River, Washington; Connecticut River, Connecticut-Massachusetts; St. Johns River, Florida) at various latitudes on the Pacific and Atlantic coasts of North America peak at water temperatures of 15.5° to 20.0°C (Leggett and Whitney 1972).

The rate of development of shad eggs is linearly related to temperature (Mansueti and Kolb 1953). Eggs hatch in 8 to 12 days at 11° to 15°C; 6 to 8 days at 17°C and 3 days at 24°C. (Leim 1924; Bigelow and Schroeder 1953; Scott and Crossman 1973). Eggs stop developing when water temperatures drop to 7°C (Leim 1924). Abnormalities develop when the temperature rises to 22°C (Leim 1924), and no viable larvae develop from eggs at water temperatures above 29°C (Bradford et al. 1966).

The American shad is intolerant of cold water temperatures. The lower thermal tolerance limit is about 2°C but prolonged exposure to 4° to 6°C may cause high mortality or stress (Chittenden 1972). If young shad are given a choice, they generally avoid temperatures below 8°C and strongly avoid temperatures below 5°C. Chittenden concluded that cold water releases below large impoundments may curtail or destroy historical spawning and nursery areas there.

Juvenile American shad attempt to avoid excessively high or rapid increases in water temperature. Tests in tanks show that shad avoid temperature increases of about 4°C above the acclimation temperature (Moss 1970). They did not attempt to avoid changes of 1°C, suggesting a sensory threshold of between +1° and +4°C above ambient temperature.

Field observations bear out the laboratory findings of Chittenden (1972) and Moss (1970). Migrations of

American shad in the ocean and freshwater are closely tied to changes in water temperature. Shad are most frequently caught commercially in ocean bottom temperatures of 7° to 13°C (Neves and Depres 1979).

Oxygen

The American shad require well-oxygenated waters either in rivers or in the sea. Dissolved oxygen levels must be at least 4 to 5 mg/l in headponds through which shad pass in their migration (Jessop 1975). In the laboratory, equilibrium is lost at dissolved oxygen levels below 3 mg/l; heavy mortality occurs at levels below 2 mg/l; and all fish die at concentrations less than 0.6 mg/l (Chittenden 1969). Shad eggs were absent where the concentration of dissolved oxygen was lower than 5 mg/l (Marcy 1976). The oxygen LC_{50} for Connecticut River shad eggs is 2.0 to 2.5 mg/l (Carlson 1968).

Turbidity

Extensive dredging of the Hudson River produced no measurable adverse effects on shad abundance (Talbot 1954). Adult shad readily enter the Shuebenacadie River in Nova Scotia, where suspended sediment concentration sometimes is 1 g/l (Leim 1924). In a laboratory study, mortality of eggs held in concentrations of suspended sediments up to 1 g/l from fertilization to hatching did not differ significantly from control groups (Auld and Schubel 1978); however, the survival of shad larvae exposed to concentrations greater than 0.1 g/l for 96 hours was sharply reduced. Larvae apparently are much less tolerant of suspended sediments than eggs.

Substrate

Substrate type apparently is unimportant to shad. They spawn in the water column and the eggs are carried downstream. American shad have been observed to spawn successfully over silt, mud, sand, gravel, and boulders (Mansueti and Kolb 1953; Walburg 1960; Leggett 1976). Only under the most adverse of conditions, in which mud covered and smothered the eggs, was substrate a problem.

Depth

American shad show little depth preference in freshwater. Adults are caught during spawning runs in all parts of the river channel. Spawning has been observed in rivers at depths ranging from 0.45 to 7 m (Mansueti and Kolb 1953; Walburg 1960; Kuzmeskus 1977).

Juveniles were found at depths of 0.9 to 4.9 m in the Connecticut River (Marcy 1976). Abundance was related to the distance upstream and not to depth. During the day, 87% of the juvenile shad caught in a gill net were near the bottom at depths of 3.7 to 4.9 m. At night, all were caught near the surface. At sea, shad are near the bottom during the day and disperse in the water column at night (Neves and Depres 1979).

Water Movement

Water velocity is critical to shad because shad must negotiate river currents and occasional fishways when migrating upstream, and pass safely over spillways while going downstream. Adult shad migrating upstream are reluctant to use traditional fishways, probably because entrance widths, depths, and flows are often unsuitable (Walburg and Nichols 1967). Pool-and-weir fishways, vertical-baffle fishways, and elevators are better carriers of American shad. For the pool-and-weir fishway, optimum difference in pool elevations is 23 cm when water velocities are 61 to 91 cm/sec. For any fish passage to work, proper current at the entrance is essential.

In the Connecticut River, the daily movement upstream is about 5 km in brackish water, and 14 km in freshwater (Leggett 1976). Adult downstream migration depends on water currents and the pattern of currents around obstructions. In the Farmington River, a tributary of the Connecticut River, flow rate into the fishway accounts for 60% of the variation in the number of downstream migrants entering the fishway (Moffitt 1979). No fish entered the tributary because of the lack of an adequate attractant flow. Fish that fail to find the downstream passage must pass over the spillway or through hydroelectric turbines. Between 57% and 80% of juvenile shad that pass through a 850 kw Ossberger turbine are killed outright, and others may die later of stress or are easy prey to predators (Gloss 1982). A fishway may cause mortality because of excessive loss of scales and injury. At least 25% of the shad die as a result of the fish-lift at Mactaquac, New Brunswick (Jessop 1975). Exposure to lethal nitrogen supersaturated waters below the dam sometimes causes stress or mortality (MacDonald and Hyatt 1973).

Spawning takes place in water velocities ranging from 9.5 to 132 cm/sec based on hydrographic data at sites where Kuzmeskus (1977) found fresh spawn. Spawning normally takes place at velocities of 30 to 90 cm/sec (Walburg 1960).

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries on the taxonomy, morphology, distribution, life history, and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. The depleted populations of the American shad, Alosa sapidissima, are being restored in many of the rivers along the east coast that originally supported large runs. The American shad is an anadromous fish that lives several years in the ocean and returns to its natal river to spawn in the spring when temperatures reach 12 °C. The eggs are carried by currents downstream from spawning sites in large rivers for 8-12 days until they hatch. The larvae, which metamorphose to juveniles in 3-4 weeks, remain in the river until fall when they migrate to the sea. Shad move offshore and southward during winter at water temperatures of 3-15 °C. American shad feed on zooplankton. They adapt readily to fresh or saltwater, but they prefer salinities exceeding 4 ppt.

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